THE GENERA OF ANCHONIEAE (HESPERIDEAE) (CRUCIFERAE; BRASSICACEAE) IN THE SOUTHEASTERN UNITED STATES[1,2]

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Tribe **Anchonieae** A. P. de Candolle, Syst. Nat. **2:** 152. 1821.

Annual, biennial, or perennial herbs [rarely shrubs]; trichomes unicellular, eglandular, simple or furcate, stellate, dendritic, or malpighiaceous, sometimes mixed with multicellular glandular ones. Inflorescences ebracteate [rarely bracteate], corymbose racemes [rarely panicles], usually elongated in fruit. Sepals erect, free or sometimes connivent, usually unequal and slightly to conspicuously saccate at base. Stamens 6, often strongly tetradynamous; median filaments free [rarely connate], unappendaged [or dentate]. Fruits dehiscent or indehiscent and usually lomentaceous, breaking into 1-seeded parts [rarely nutlike], terete, tetragonal, or flattened parallel [or at right angles] to the septum; styles conspicuous [or obsolete]; stigmas strongly 2-lobed [rarely entire], the lobes connivent or spreading, decurrent or not [rarely forming conspicuous horns or appendages]. Seeds few to numerous, uniseriately [or biseriately] arranged in each locule, wingless [or winged], nonmucilaginous [sometimes mucilaginous] when wet; cotyledons accumbent or incumbent. (Including Buniadeae DC., Cheirantheae Webb & Berth., Erysimeae Dumort., Hesperideae Prantl, Matthioleae O. E. Schulz.) Type genus: *Anchonium* DC.

[1]Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and currently supported by BSR-8415769 (C. E. Wood, Jr., principal investigator), under which this research was done, and BSR-8415637 (N. G. Miller, principal investigator). This account, the 121st in the series, follows the format established in the first paper (Jour. Arnold Arb. **39:** 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets. The references that I have not verified are marked with asterisks.

I am most grateful to Carroll Wood for his continuous support, advice, and help during the preparation of this paper, and particularly for his critical review of the manuscript. I should also like to thank Norton G. Miller for reviewing the paper, Reed C. Rollins and Robert A. Price for their valuable discussions, and Barbara Nimblett for typing the manuscript. I am grateful to Elizabeth B. Schmidt and Stephen A. Spongberg for their editorial advice.

[2]For an account of the family and its tribes, see Al-Shehbaz, The Tribes of Cruciferae (Brassicaceae) in the Southeastern United States. Jour. Arnold Arb. **65:** 343–373. 1984.

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Journal of the Arnold Arboretum **69:** 193–212. July, 1988.

As delimited here, the Anchonieae are a well-defined group of about 27 genera (eight monotypic) and some 240 species that have multicellular glandular trichomes and/or connivent, decurrent stigmatic lobes. *Hesperis* L. (ca. 25 species), *Malcolmia* R. Br. (including *Strigosella* Boiss.; 35 species), and *Matthiola* R. Br. (50 species) are the core genera of the tribe. These and 14 others were placed by Schulz in the Hesperideae and the Matthioleae, while the remainder either were assigned by him to other tribes (e.g., *Bunias* L. in the Euclidieae DC. and *Dontostemon* Andrz. in the Arabideae DC.) or were described after the publication of his monograph. *Atelanthera* J. D. Hooker & Thomson, *Cryptospora* Karelin & Kirilov, *Hesperidanthus* (Robinson) Rydb., *Iodanthus* Torrey & A. Gray ex Steudel, *Maresia* Pomel, *Mathewsia* W. J. Hooker & Arnott, *Notoceras* R. Br., *Pseudocamelina* (Boiss.) Busch, *Tetracme* Bunge, *Thelypodiopsis* Rydb., and *Thelypodium* Endl. have all been excluded from the Hesperideae and the Matthioleae sensu Schulz and assigned to other tribes (Al-Shehbaz, 1973, 1988; Dvořák, 1970, 1972; Miller; Rollins, 1966). *Aubrieta* Adanson (12 species; southwestern Asia, Balkan Peninsula), *Blennodia* R. Br. (two species; Australia), *Pycnoplinthopsis* Jafri (monotypic; Bhutan), *Pycnoplinthus* O. E. Schulz (monotypic; Himalayan region), and *Solms-Laubachia* Muschler (13 species; China), which have been retained in the Hesperideae or the Matthioleae by various workers, should also be excluded from the Anchonieae because they are not related to any of its members and they lack the characteristic stigmas or glands.

Schulz distinguished the Hesperideae from the Matthioleae on the basis of cotyledonary position. However, this distinction is clearly artificial since both accumbent and incumbent cotyledons are found within numerous genera of the Cruciferae. It is evident that this feature is unreliable in tribal delimitation.

The number of genera and species estimated here for the Anchonieae differs markedly from that of Al-Shehbaz (1984) for the Hesperideae because it does not include *Erysimum* L. sensu lato (ca. 200 species) or the genera that I have excluded from the Anchonieae. None of the excluded genera has glandular trichomes, and their stigmatic lobes are neither decurrent nor connivent. They have been assigned to the tribes Erysimeae and Sisymbrieae DC. (Dvořák, 1972), but their proper disposition may be in the latter tribe. In fact, the presence of cardenolides (see below) in both *Erysimum* sensu lato and *Sisymbrium* L. strongly supports their placement in one tribe. I am following my earlier account (Al-Shehbaz, 1984) by retaining *Erysimum* in the Anchonieae, but careful evaluation of the tribal disposition of this and the many excluded genera is needed. It is beyond the scope of this flora to undertake such a task.

Within the Cruciferae multicellular glandular trichomes are apparently unique to the Anchonieae. Unicellular glandular trichomes are found only in *Descurainia* Webb & Berth., which is evidently unrelated to any member of this tribe. The absence of glandular trichomes among some members of the Anchonieae is probably a derived state. The genera *Dontostemon, Hesperis, Matthiola,* and *Parrya* R. Br. include species both with and without glandular structures, while *M. longipetala* (Vent.) DC. and *P. nudicaulis* (L.) Regel have glandular or eglandular plants within the same population.

Anchonieae is the earliest legitimate, validly published name for the tribe that includes *Anchonium.* However, recent students of the Cruciferae place the genus in the tribe Hesperideae even though this name was published 70 years later. All of De Candolle's (1821) tribes of the Cruciferae are perfectly acceptable, and many were recognized by Von Hayek, Hooker (in Bentham & Hooker), Janchen, and Schulz. Avetisian united the Anchonieae (as the Hesperideae) with six other tribes that she placed in the Sisymbrieae. However, this action was inappropriate.

The Anchonieae are distributed primarily in the Old World (Eurasia, northern and tropical Africa); only the range of the *Parrya nudicaulis* complex extends into North America. Dvořák (1972) has considered Pacific North America and northeastern Asia as one evolutionary center for the tribe (as Hesperideae) and central Asia as another. It is very likely, however, that the occurrence of *Parrya* in the New World represents a recent migration.

The Anchonieae sensu lato (43 genera and ca. 500 species; Al-Shehbaz, 1984) are represented in the southeastern United States by three genera and five species, one of which is indigenous.

Chromosome numbers in the Anchonieae sensu stricto (i.e., excluding *Erysimum* and many other somewhat related genera) are known for 18 genera and 88 species (about 37 percent of the tribe). Nearly 77 percent of the species surveyed are diploid, and only about 15 percent are exclusively polyploid. About 45 percent of the species have chromosome numbers based on seven, 30 percent on six, and only 13 percent on eight (author's compilation). The lowest chromosome number ($2n = 10$) has recently been reported for the monotypic *Lonchophora* Durieu (Carrique & Martínez), which is endemic to northwestern Africa. *Diceratella* Boiss. (seven species; tropical eastern Africa, Socotra, southern Iran), *Morettia* DC. (four species; northern Africa, Somalia, Israel, Arabia), and *Parolinia* Webb (five species; Canary Islands) are all diploid with $2n = 22$. They are closely related to *Matthiola,* in which only one species is known to have such a number, and at least 20 others are diploids with $2n = 12$. It is very likely that the base chromosome number for *Matthiola* is six, and that seven and eight, which are rare in the genus, are derived.

The Anchonieae have been poorly studied phytochemically, and the scant data do not provide patterns of potential chemotaxonomic significance. A thorough survey of cardenolides and mustard oils for the many genera that I exclude from the Anchonieae may aid in the adjustment of their tribal placement.

Hooks, spines, wings, hornlike appendages, and sharply pointed beaks on the fruits evidently help in dispersal. These structures are found in *Bunias, Diceratella, Lonchophora, Matthiola, Parolinia,* and *Veselskya* Opiz (= *Pyramidium* Boiss.). Lomentaceous fruits with corky walls are characteristic of most species of *Anchonium, Chorispora* DC., and *Sterigmostemum* Bieb., but the dispersal values of such features are not fully understood. The abundance of glands on the fruits of many species may have defensive rather than dispersal significance.

Except for a few ornamental and several weedy species (see below), the tribe has no economic importance.

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Key to the Genera of Anchonieae in the Southeastern United States[4]

A. Multicellular glandular trichomes or papillae usually present; plants without malpighiaceous or 3- to 5-forked, sessile, appressed, medifixed trichomes; stigmatic lobes decurrent, connivent or connate.
  B. Fruits beaked, indehiscent, lomentaceous, often breaking transversely at maturity into 1- or 2-seeded segments; plants with multiseriate, numerous-celled glandular papillae. ..... 37. *Chorispora.*
  B. Fruits beakless, dehiscent, not lomentaceous; plants with uniseriate, few-celled glandular trichomes. ..... 38. *Hesperis.*
A. Multicellular glandular trichomes or papillae absent; plants with malpighiaceous or 3- to 5-forked, sessile, appressed, medifixed trichomes; stigmatic lobes neither decurrent nor connivent, usually divergent. ..... 39. *Erysimum.*

37. **Chorispora** R. Brown ex A. P. de Candolle, Syst. Nat. **2:** 435. 1821, nom. cons.

Annuals [or caespitose perennials with thick, branched or unbranched caudices], almost always with stipitate, multicellular, multiseriate glands, these often mixed with unicellular, unbranched trichomes [rarely glabrous]. Stems simple or most commonly branched at base. Basal leaves petiolate, usually not forming a distinct rosette, dentate, sinuate, runcinate [or pinnatisect]; cauline leaves smaller, less divided [sometimes lacking]. Flowers in ebracteate, corymbose racemes [sometimes solitary on long scapes]; infructescences elongated; fruiting pedicels divaricate [rarely erect or deflexed], stout and nearly as wide as the fruit [or slender and much narrower]. Sepals linear to narrowly oblong [or ovate], erect, somewhat connivent, sparsely [to densely] covered with glandular papillae [or eglandular trichomes], rounded at apex, usually membranaceous at margin, the inner pair strongly saccate at base. Petals purple, rose, lavender [white or yellow], strongly differentiated into blade and claw, 2–3 times longer than the sepals; blades oblong to spatulate [or broadly obovate], rounded [or retuse to emarginate] at apex. Lateral nectar glands horseshoe shaped to ringlike, median glands absent. Stamens 6, tetradynamous; filaments erect, linear, unappendaged; anthers exserted, linear [oblong or ovate], sagittate at base. Fruits linear [oblong or lanceolate], terete, indehiscent, beaked, corky, lomentaceous, smooth to slightly [or strongly] torulose [or moniliform], glabrous or with glandular papillae, breaking into segments; segments 1-seeded, closed, with a

[4]The genera are numbered as in the treatment of the tribes of Cruciferae in the southeastern United States (Jour. Arnold Arb. **65:** 343–373. 1984). Genera 1 and 2 (Thelypodieae) appeared in *ibid.* **66:** 95–111. 1985; genera 3–13 (Brassiceae) in *ibid.* 279–351; genera 14–19 (Lepidieae) in *ibid.* **67:** 265–311. 1986; genera 20–26 (Alysseae) in *ibid.* **68:** 185–240. 1987; and genera 27–36 (Arabideae) in *ibid.* **69:** 85–166. 1988.

thick, corky or woody wall, of which the outer portion is derived from the valve and the inner from the septum; beaks subulate [to filiform], seedless, gradually tapered to the apex, nearly as long as [or much shorter than] the seed-containing part; replums persistent; stigmas with 2 decurrent lobes; septum firm, thick. Seeds uniseriately arranged, oblong, strongly compressed, wingless, embedded in cavities of the septum, nonmucilaginous when wet; cotyledons accumbent. Base chromosome numbers 7, 9. (Including *Chorispermum* R. Br.) TYPE SPECIES: *Raphanus tenellus* Pallas = *C. tenella* (Pallas) DC. (Name from Greek *choris,* asunder, and *spora,* seed, in reference to the fruits that break at the constrictions into one-seeded segments.)

A well-defined genus of about 13 species, all of which are indigenous to southwestern and central Asia. The weedy *Chorispora tenella,* blue mustard, $2n = 14$, is sporadically naturalized throughout most of the Northern Hemisphere, as well as in parts of South America. It is widely distributed in southern Canada and in most of the Mountain and Pacific states. It has been reported from Tennessee, Louisiana, and Arkansas.

Chorispora is easily distinguished by its multicellular glandular papillae, decurrent stigmas, persistent replums, and beaked, indehiscent, corky, lomentaceous fruits that break up at maturity into one-seeded segments. Von Hayek and Schulz both associated *Chorispora* with *Diptychocarpus* Trautv. (monotypic; Afghanistan, Iran, Pakistan, central Asia), which differs in having winged seeds and dimorphic fruits (dehiscent upper ones and indehiscent, lomentaceous, corky lower ones). Dvořák (1972), on the other hand, has suggested that *Chorispora* and *Sterigmostemum* (seven species; central and southwestern Asia) were derived from a common ancestor.

Little is known about reproductive biology in species of *Chorispora,* which vary widely in flower size and color (bright yellow to deep purple). The weedy *C. tenella* has the smallest flowers (petals to 1 by 0.5 cm) and is likely to be self-compatible, while *C. Bungeana* Fischer & Meyer (Afghanistan, Pakistan, central Asia) has the largest flowers (petals to 2.5 by 1 cm). Flowers of all species of *Chorispora* have well-developed lateral nectar glands, and their lateral sepals are strongly saccate at the base. They produce abundant nectar and pollen and are therefore well adapted to cross-pollination.

Chromosome numbers are known for only three species. *Chorispora persica* Boiss. (Iran) and *C. tenella* both have $2n = 14$, whereas *C. iberica* (Bieb.) DC. (Caucasus, Iran, Turkey) has $2n = 18$ (Aryavand, 1975, 1983; Dvořák & Dadáková; Rodman & Bhargava). The closely related *Diptychocarpus* has $2n = 14$.

The chemistry of the genus is poorly surveyed, and only *Chorispora tenella* has been analyzed for leaf glucosinolates. It has high concentrations of allyl-glucosinolate and lower ones of 3-methylthiopropyl and 3-methylsulfinylpropyl glucosinolates (Rodman & Chew). Females of the butterfly *Pieris napi* deposit their eggs on the toxic *C. tenella,* failing to discriminate between it and the nontoxic native North American Cruciferae. Rodman & Chew have suggested that the isothiocyanate derivative of the last compound is probably responsible for the mortality of larvae that feed on this plant.

The seed coat of *Chorispora tenella* consists of flattened epidermal cells and thin-walled palisade cells (Vaughan & Whitehouse).

Except for the weedy *Chorispora tenella,* the genus has no economic value. The fruits of *C. elegans* Camb. (as *C. sabulosa* Camb.) are said to be eaten either raw or cooked by the poorer people in northern Pakistan (Jafri).

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38. **Hesperis** Linnaeus, Sp. Pl. **2.** 663. 1753; Gen. Pl. ed. 5. 297. 1754.

Biennial or perennial herbs with unicellular, eglandular, unbranched or furcate [to stellate] trichomes, these often mixed with multicellular, uniseriate glandular ones. Basal leaves petiolate, dentate [to pinnately lobed]; cauline leaves short-petiolate [or sessile and sometimes auriculate to amplexicaul]. Inflorescences ebracteate [or bracteate], corymbose [or elongated] racemes [or panicles], greatly expanded in fruit; flowers large, showy, fragrant; base of flowering pedicels with a large gland on each side; fruiting pedicels divaricate [to reflexed], slender [or stout and nearly as thick as the fruit]. Sepals erect and somewhat connivent [rarely spreading], oblong, unequal [rarely equal], the lateral (inner) pair strongly saccate at base. Petals white, lavender, pink, purple, violet [yellow, brown, or greenish], often with darker colored veins, about twice as long as the sepals, strongly differentiated into blade and claw; blades obovate [to oblong], rounded at apex; claws erect, flattened. Lateral nectar glands ringlike or horseshoe shaped, median glands absent. Stamens 6, strongly tetradynamous; filaments linear, erect, not appendaged, the median pair usually dilated [or slightly winged] at base; anthers linear [or oblong], strongly sagittate at base. Fruits linear, terete [rarely flattened or 4-angled], torulose, dehiscent [or indehiscent], often attenuate at apex; valves with a prominent midvein, glabrous or pubescent with eglandular [or glandular] trichomes; styles short to obsolete; stigmas strongly 2-lobed, the lobes connivent, sometimes decurrent. Seeds many, oblong, wingless, uniseriately arranged, usually nonmucilaginous when wet; cotyledons incumbent. Base chromosome numbers 6, 7, 8, 10. (Including *Deilosma* Spach, *Kladnia* Schur, *Micrantha* Dvořák.) LECTOTYPE SPECIES: *H. matronalis* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **2:** 175. 1913. (Name from old Greek, *hesperos,* evening, in reference to the time when flowers of certain species are most fragrant.)—DAME'S VIOLET, DAME'S ROCKET.

A well-marked, but taxonomically difficult Old World genus of about 25 species. The higher estimate of 60 species by Dvořák (1980), which I (Al-Shehbaz, 1984) have accepted, is evidently exaggerated. The center of greatest diversity, where about 70 percent of the species of *Hesperis* are endemic, includes the Balkan Peninsula, Turkey, Iran, and the Caucasus. The genus is poorly represented in eastern Asia and northern Africa and is absent from the Southern Hemisphere. A single species, *H. matronalis,* dame's violet, dame's rocket, rocket, $2n = 24$, is a cultivated ornamental plant and a naturalized weed in many parts of the world. It is sporadically distributed in the southeastern United States, where it has been reported from North Carolina, Georgia, Tennessee, and Arkansas. It usually grows along roadsides and in rich, moist woodlands and old gardens.

Hesperis matronalis has been divided into several subspecies on the basis of differences in flower color, petal length, and trichome type (Ball; Cullen). These

taxa are artificially delimited and unsatisfactory because they are based on characters that usually intergrade within many populations. Therefore, I am not recognizing any infraspecific taxa among the North American populations of *H. matronalis*.

The infrageneric classification of *Hesperis* is evidently controversial, for there is a lack of agreement among the several accounts consulted. De Candolle (1821) recognized 22 species, of which two were placed in sect. HESPERIS (as sect. *Hesperidium* DC.) (petal limb linear) and the remainder in sect. DELIOSMA Andrz. ex DC. (petal limb obovate). Tzvelev, on the other hand, placed the 18 species growing in the Soviet Union in three sections and two series, while Dvořák (1968a) assigned the 11 species growing in Iran to two subgenera and two sections. Finally, Dvořák (1973) recognized 31 species in five subgenera that were defined mainly by the presence of bracts and the degree of fruit dehiscence. The infrageneric taxa above are doubtfully practical, and they do not represent natural subdivisions of *Hesperis*.

Hesperis has been variously associated with *Blennodia, Clausia* Trotzky, *Iodanthus, Malcolmia, Parrya,* and *Sterigmostemum*. Contrary to what Von Hayek and Schulz have suggested, the genus is evidently unrelated to either *Blennodia* or *Iodanthus* and is closest to *Clausia* and *Sterigmostemum*. From all these genera, *Hesperis* is easily distinguished in having terete, torulose, dehiscent or indehiscent fruits; incumbent cotyledons; furcate to stellate trichomes usually mixed with glandular ones; free median staminal filaments; and large, odoriferous flowers.

Perhaps one of the most controversial taxonomic problems in *Hesperis* is species delimitation. The majority of the approximately 300 binomials listed in *Index Kewensis* are now assigned to other genera. Many species have been described on the basis of characters with poorly understood variations, while others represent local populations of highly variable species. In the absence of a thorough monographic account for the whole genus, it is advisable to recognize only about 25 species. Although natural interspecific hybridization has been reported a few times (Dvořák, 1965, 1967a), it is highly unlikely that it has played a major role in obscuring the species boundaries.

Chromosome numbers have been reported for about 14 species, four of which are tetraploids ($x = 6, 7$) that belong to the *Hesperis matronalis* complex. The karyotype of this species consists of eight metacentric pairs of chromosomes, two, one, or no submetacentric pairs, and two, three, or four subtelocentric pairs (Bhattacharyya; Dvořák & Dadáková, 1976; Gohil & Raina). Because of associations among four pairs of chromosomes, Gohil & Raina concluded that *H. matronalis* is a segmental allopolyploid and a complex translocation heterozygote. Despite the presence of multivalent associations at metaphase I, meiosis was quite regular and pollen stainability was more than 90 percent. Counts of $2n = 26$ and 28 for *H. matronalis* need careful evaluation; those of $2n = 32$ (e.g., Easterly) are probably erroneous. Furthermore, reports of $2n = 14$ are evidently based on plants of other species. Aneuploidy and tetraploidy ($x = 10$) have been reported for *H. sylvestris* Crantz and *H. ovata* Dvořák, respectively. The eight remaining species are all diploid based on seven or eight.

The reproductive biology of *Hesperis* is poorly understood. Bateman reported self-incompatibility in one species without providing a name. Several species have dull-colored flowers and are apparently pollinated at night by moths, as is *H. tristis* L. (Faegri & Van der Pijl).

Only *Hesperis matronalis* has been surveyed for sterols (Knights & Berrie), fatty acids (Appelqvist, 1971, 1976), and glucosinolates (Christensen & Kjaer; Cole). It contains 4-methylthiobutyl and 6-methylsulfinylhexyl glucosinolates, but allylglucosinolate, reported by Daxenbichler and colleagues, has not been detected by other workers. The seeds contain high concentrations of linolenic, linoleic, and oleic acids (ca. 51–55, 22–24, and 13–14 percent, respectively) but no traces of erucic acid.

The seed coat of *Hesperis matronalis* consists of an epidermis with central swellings that protrude from the outer wall into the lumena of larger cells, a subepidermis with tangentially elongated cells, and a palisade layer with radially elongated cells, the inner tangential walls of which are flattened (Vaughan & Whitehouse).

Except for *Hesperis matronalis,* which is an ornamental and an escape from cultivation, the genus has no economic value.

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39. **Erysimum** Linnaeus, Sp. Pl. **2:** 660. 1753; Gen. Pl. ed. 5. 296. 1754.

Annual, biennial, or perennial herbs [sometimes subshrubs or shrubs]; trichomes always sessile, medifixed, appressed, 2-fid (malpighiaceous) or 3- to 5-(to 7-)fid (stellate). Lower leaves petiolate, entire to dentate, rarely pinnatifid [or pinnatisect]; cauline leaves short-petiolate to sessile [very rarely auriculate]. Inflorescences ebracteate, terminal, corymbose racemes, greatly elongated in fruit. Sepals oblong to linear, erect, densely pubescent, the lateral pair saccate at base. Petals orange to bright yellow [creamy white, lavender, pink, violet,

or purple], strongly differentiated into limb and claw; limbs broadly to narrowly obovate [or oblong]; claws erect, nearly as long as the sepals. Lateral nectar glands ringlike or horseshoe shaped, encircling or subtending the bases of lateral stamens; median glands present [or absent]. Stamens 6, strongly tetradynamous; filaments free, linear, unappendaged, sometimes dilated at base; anthers linear to oblong, sagittate at base. Fruits linear [very rarely oblong], terete, tetragonal [or slightly to strongly compressed parallel, or at right angles, to the septum], smooth [rarely torulose], quickly or tardily dehiscent; valves with a prominent midvein, always pubescent on the outside, very rarely so on the inside; styles obsolete to conspicuous [only rarely subequaling or half as long as the fruit]; stigmas 2-lobed, the lobes neither decurrent nor connivent. Seeds oblong, terete [or flattened], wingless [winged or marginate], uniseriately [rarely subbiseriately] arranged in each locule of the fruit, nonmucilaginous when wet; cotyledons incumbent [to accumbent]. Base chromosome numbers 6–11, 13, 15, 17. (Including *Acachmena* H. P. Fuchs; *Agonolobus* (DC.) Reichenb.; *Cheiranthus* L.;[5] *Cheiri* Ludwig; *Cheirinia* Link; *Cuspidaria* (DC.) Besser (1822) non DC. (1838, nom. cons.); *Dichroanthus* Webb & Berth.; *Erysimastrum* (DC.) Rupr.; *Mitophyllum* O. E. Schulz (1933) non Greene (1904); *Rhammatophyllum* O. E. Schulz; *Strophades* Boiss.; *Stylonema* (DC.) Kuntze (1891) non Reinsch (1874); *Syrenia* Andrz. ex Besser; *Syreniopsis* H. P. Fuchs (1959) non *Syrenopsis* Jaub. & Spach (1842); *Zederbauera* H. P. Fuchs.) LECTOTYPE SPECIES: *E. cheiranthoides* L.[6] (Name probably from old Greek used by Hippocrates, Theophrastus, and others for plants possibly of this genus. Fernald, however, maintained that the generic name is derived from Greek *eryomai,* help or save, from the supposed medicinal properties of certain species.)—BLISTER CRESS, TREACLE MUSTARD, WALLFLOWER.

A well-defined and taxonomically difficult genus of about 200 species (see below for different estimates) restricted to the Northern Hemisphere, with the centers of greatest endemism being the Middle East (Turkey through Iran and Afghanistan; ca. 80 species), southern Europe (ca. 50), and central Asia (20). At least 15 species of *Erysimum* grow in more than one of the areas above; 12 are endemic to North America (Price), four to North Africa, and five to the Canary Islands, Madeira, and the Cape Verde Islands. The genus is represented in the southeastern United States by four species, of which one is indigenous, one is a widely cultivated ornamental, and two are cosmopolitan weeds.

Erysimum capitatum (Douglas ex W. J. Hooker) Greene (*Cheiranthus capitatus* Douglas ex W. J. Hooker), $2n = 36$, is the most variable and widely distributed of all the North American species. Of the nine subspecies recognized

[5]*Erysimum* and *Cheiranthus* were simultaneously described by Linnaeus (Sp. Pl. **2:** 660, 661, respectively, 1753). Wettstein, who was the first to unite the two genera, adopted *Erysimum* for the combined genus; consequently, this name has priority (see ICBN Article 57.2, 1983).

[6]Scopoli (Fl. Carniol. ed. 2, **2:** 27–29. 1772) had effectively lectotypified *Erysimum* by transferring the other original Linnaean species (Sp. Pl. **2:** 660, 661. 1753) to *Sisymbrium* L. while retaining *E. cheiranthoides* in *Erysimum*. Several North American authors (e.g., Britton & Brown; Greene) chose this species as the type of *Cheirinia* and treated *Erysimum* as a small (perhaps monotypic) genus, the type species of which is *E. officinale* (now universally recognized as *S. officinale* (L.) Scop.).

by Price, only subsp. *capitatum* occurs in the Southeastern States (DeKalb, Putnam, and Smith counties, Tennessee; Faulkner and Logan counties, Arkansas). From here the subspecies is distributed westward into the Southwestern and Pacific states and also grows in Idaho (Price). Subspecies *capitatum* is easily distinguished from the other taxa of *Erysimum* that grow in the Southeast by its orange petals to 3 cm long, erect to ascending fruits on thick fruiting pedicels, and fruit valves with the inner surfaces glabrous. Small's (1933) report of *E. asperum* (Nutt.) DC. (as *Cheirinia*) from Tennessee was evidently based on a misidentification of plants of *E. capitatum*.

Erysimum cheiranthoides L. (*Cheirinia cheiranthoides* (L.) Link, *E. parviflorum* Pers.), wormseed mustard, $2n = 16$, is a Eurasian weed widely naturalized in North America. It occurs in North Carolina, Florida, Tennessee, and Arkansas, where it grows in waste grounds, pastures, disturbed sites, grainfields, and hillsides, as well as along roadsides. Ahti and Ball recognized two subspecies in *E. cheiranthoides*; only the type subspecies is naturalized in the United States. *Erysimum cheiranthoides* is readily distinguished from the other North American species of the genus by its fruits 1.5–2.5 mm long, conspicuously pubescent inner valve surfaces, fruiting pedicels much more slender than the fruits, and yellow petals 3.5–5.5 mm long.

Erysimum repandum L. (*Cheirinia repanda* (L.) Link, *E. rigidum* DC.), treacle mustard, $2n = 16$, is another Eurasian weed widely distributed in North America. It has been reported from all of the Southeastern States but South Carolina, Georgia, and Florida, where it is likely to be found. It is an annual with widely spreading, somewhat quadrangular, slightly torulose fruits 4–8 cm long; divaricate, stout fruiting pedicels nearly as thick as the fruit; and yellow petals 6–8 mm long.

Small (1913) listed *Erysimum inconspicuum* (S. Watson) MacM., $2n = 54$, for Arkansas, but the record is highly unlikely because the species is indigenous to western North America and is adventive only in some of the Midwestern States. *Erysimum Cheiri* (L.) Crantz (*Cheiranthus Cheiri* L.), wallflower, $2n = 12$, which is grown as an ornamental throughout the Southeastern States, does not seem to have escaped from cultivation anywhere in North America.

The infrageneric subdivisions of *Erysimum* that were recognized by Busch, De Candolle (1821, 1824), and Wettstein have not been widely accepted. Busch, for example, placed the 51 species growing in the Soviet Union in two sections (one monotypic) divided into 18 series. A close examination of *Erysimum* on a worldwide basis reveals that convergent evolution has probably occurred repeatedly in features such as position of the cotyledons, presence of the seed wing, flattening of the fruit valve, color of the flower, and type of trichomes. Therefore, it is quite difficult, if not impossible, to delimit natural subdivisions within the genus.

Only two of the many generic segregates of *Erysimum* require critical evaluation. *Cheiranthus* has been distinguished from *Erysimum* in several recent floras (e.g., Ball; Townsend) on the basis of having strongly flattened fruits, accumbent cotyledons, subbiseriately arranged seeds, and no median nectaries. *Erysimum*, on the other hand, is said to differ in having terete, quadrangular, or slightly flattened fruits, incumbent cotyledons, uniseriate seeds, and well-

developed median nectaries. As shown by Snogerup (1967a) and Price, however, all of these alleged differences are unreliable; they break down within various species complexes of *Erysimum*.

The systematic position of *Syrenia* is problematic. The genus is distinguished from *Erysimum* in having slender styles that are subequal to the oblong fruits, transversely oriented malpighiaceous trichomes on the fruit valves, and no median nectaries. Long styles are found in several species of *Erysimum* (e.g., *E. cuspidatum* (Bieb.) DC.) that lack the transversely oriented fruit trichomes. Price (p. 6) suggested that *Syrenia* is "apparently either a sister group to or a derivative of *Erysimum*." I prefer to unite *Syrenia* with *Erysimum*, as has been done by Polatschek (1982).

Erysimum is perhaps the most taxonomically difficult genus in the Cruciferae. It is much in need of a comprehensive treatment. Specimens without a combination of adequate flowers, fruits, and basal leaves are often difficult to identify. Collectors should also make notes on the shape of the cross section of fresh fruits. Many authors (e.g., Busch; Jafri; Schulz; Townsend) have estimated about 80 to 100 species in *Erysimum*, but the actual number is nearly twice that. However, Polatschek (1986) has suggested that the genus contains between 350 and 420 species. Evidently, species delimitation in *Erysimum* is highly controversial. Numerous "species" have been described on the basis of minor variations in populations of previously recognized taxa. Species circumscription can be a nightmare because of the frequent lack of sharply defined discontinuities among the taxa of a given complex. It is not surprising, therefore, to encounter disagreements among systematists on assigning a specific or an infraspecific rank for a given taxon. A case in point is the *E. capitatum* alliance (sensu Price).

Snogerup (1967a) and Price have reported that in several species, including *Erysimum capitatum*, full stigmatic expansion and receptivity take place within a few days after anther dehiscence. These are clear-cut cases of protandry. Protogyny occurs in *E. repandum* and several other species (Al-Shehbaz). The flowers of *E. capitatum* and *E. Cheiri* are sweet scented and are up to 3 cm in diameter. They are among the largest in the Cruciferae. *Erysimum capitatum* is self-incompatible (Mulligan), while *E. Cheiri* has cryptic self-incompatibility (Bateman; Watts). Plants of *E. Cheiri* set seeds and maintain vigor and fertility even after several generations of selfing. However, various cultivars have different levels of self-incompatibility. Bateman has shown that in plants pollinated with a mixture of equal amounts of self and foreign pollen (the latter carrying a dominant allele that produces red flowers) more than 90 percent of their seed set results from cross fertilization.

On the basis of frequent meiotic irregularities, very low pollen fertility, and abundant seed set, both *Erysimum hieraciifolium* L. and *E. inconspicuum* are believed to be agamospermous (Mulligan; Mulligan & Frankton).

Chromosome numbers are known for about 100 species, of which half are diploid and about 40 percent polyploid. There is a continuous series of base chromosome numbers from six to 13, but many species (ca. 39 percent) are based on seven, 20 percent on eight, 15 percent on nine, and 13 percent on six. Both aneuploidy and polyploidy have played major roles in the evolution

of the genus. All members of the North American *Erysimum capitatum* complex are tetraploids based on nine (Price).

Polatschek (1986) has suggested that natural hybrids are not known in *Erysimum*. However, several authors (e.g., Favarger, 1964; Knobloch; Snogerup, 1967a, 1967b; Wettstein) have reported putative hybridization between *E. Cheiri* and four other species. Price, on the other hand, has found a natural hybrid involving *E. capitatum* and *E. insulare* Greene. It is evident that hybridization has been insignificant in obscuring the specific boundaries in the genus. Although species of the *E. capitatum* complex are readily crossed experimentally, they do not hybridize in nature because either they are exclusively allopatric or they occupy different habitats in areas of sympatry (Price).

Numerous species of *Erysimum* have been analyzed for fatty acids, glucosinolates (mustard-oil glucosides), and cardenolides (cardiac glycosides). The glucosinolates in most of the approximately 20 species analyzed are derived from the amino acid methionine. There is a complex array of 3-methylsulfinyl, sulfonyl, or thioalkyl glucosinolates, their higher homologues, or their hydroxylated derivatives that cyclize upon hydrolysis into oxazolidinethiones (Cole; Daxenbichler *et al.*; Kjaer & Schuster, 1970, 1973). Five species have 3-methoxycarbonylpropylglucosinolate, which appears to be unique to *Erysimum* (Al-Shehbaz & Al-Shammary). The glucosinolate profiles may be valuable in solving some of the taxonomic problems in the genus.

The cardenolides have been surveyed for at least 30 species. They are found in every species examined thus far, and it is very likely that they occur throughout *Erysimum*, including *Cheiranthus* and *Syrenia*. Their profiles appear to be useful taxonomically (Kowalewski; Latowski *et al.*; Rodman *et al.*). Because the occurrence of cardenolides in the Cruciferae seems to be restricted to *Erysimum*, *Sisymbrium* L., and *Conringia* Heister ex Fabr., a few authors (e.g., Latowski *et al.*) have suggested a closer relationship between the first two genera.

Seeds of about 15 species have been studied for fatty acids. The distribution of these compounds shows no patterns of chemotaxonomic significance, except for supporting the union of *Cheiranthus* and *Erysimum*. A similar conclusion is reached from data on sterols (Knights & Berrie), cardenolides (Latowski *et al.*), and glucosinolates (pers. obs.).

Bosbach has suggested that the distribution of rubisco (ribulose 1,5-biphosphate carboxylase-oxygenase, fraction 1 protein) is useful taxonomically in *Erysimum*. These proteins are separated into their polypeptide subunits by using polyacrylamide gel electrophoresis followed by isoelectrofocusing.

Many species of *Erysimum* are grown as ornamentals (Bailey *et al.*), but the one most widely cultivated is *E. Cheiri* (wallflower). Snogerup (1967b) suggested that *E. Cheiri* has probably evolved from hybridization between *E. Senoneri* and *E. cornithum* (Boiss.) Wettst. However, other Aegean taxa of sect. CHEIRANTHUS (L.) Wettst. that also have $2n = 12$ were not excluded. Several species of *Erysimum* are cultivated in eastern Europe, particularly in the Soviet Union, for the pharmacological utilization of their cardiac glycosides (Rodman *et al.*). At least two species, *E. repandum* and *E. cheiranthoides*, are cosmopolitan weeds. The latter is said to cause mortality of swine in Canada (Kingsbury).

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